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#### SUPPLEMENTARY MATERIALS

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Materials and Methods

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## CONSERVATION

# Recovery of large carnivores in Europe's modern human-dominated landscapes

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The conservation of large carnivores is a formidable challenge for biodiversity conservation. Using a data set on the past and current status of brown bears (*Ursus arctos*), Eurasian lynx (*Lynx lynx*), gray wolves (*Canis lupus*), and wolverines (*Gulo gulo*) in European countries, we show that roughly one-third of mainland Europe hosts at least one large carnivore species, with stable or increasing abundance in most cases in 21st-century records. The reasons for this overall conservation success include protective legislation, supportive public opinion, and a variety of practices making coexistence between large carnivores and people possible. The European situation reveals that large carnivores and people can share the same landscape.

Large carnivores are among the most controversial and challenging group of species to conserve in our modern and crowded world. There is a deeply rooted hostility to these species in human history and culture, because of perceptions of their negative impacts on human livelihoods (1). Large carnivore abundance and distribution have historically been reduced (2), and their present conservation has become intertwined with broader emotional, political, and socioeconomic issues that further complicate this challenge (3). In addition, large carnivores live at low densities and have large spatial requirements (4). Accordingly, the conservation of viable large carnivore populations needs to be planned and coordinated on very wide scales, often spanning many intra- and international borders [i.e., requiring transboundary management (5)].

The main debate around large carnivore conservation is whether there is enough suitable space

left for viable and ecologically functional populations (6). As the two main drivers of the current biodiversity crisis—human overpopulation and overconsumption—show no sign of reducing, an intuitive forecast could be that large carnivores will persist only in highly managed protected areas (with regular translocations being made to achieve artificial connectivity) or in some remote and uninhabited wilderness areas. This approach derives conceptually from the North American wilderness model that separates people and nature and that has further been adopted in many Asian, African, and neotropical countries (6) (“keeping people and predators apart,” the separation model). The ultimate expression of this approach lies in the southern African propensity to fence protected areas (6). The alternative model, “allowing people and predators together” (coexistence model), following a landscape-scale conservation approach, has rarely been given proper consideration, probably because

it has been deemed a priori to fail because of the existing conflicts between large carnivores and humans. This dichotomy of large carnivore conservation models is analogous to the land-sharing versus land-sparing debate, which is ongoing in a wider biodiversity conservation context (7).

We compiled data about the status (i.e., current and past occurrence and abundance) of large carnivores [brown bears (*Ursus arctos*), Eurasian lynx (*Lynx lynx*), gray wolves (*Canis lupus*), and wolverines (*Gulo gulo*)] in Europe (8). We show that the European continent (considering all continental European countries excluding Belarus, Ukraine, and Russia) is succeeding in maintaining, and to some extent restoring, viable large carnivore populations on a continental scale (Fig. 1 and fig. S1). All mainland European countries except for Belgium, Denmark, the Netherlands, and Luxembourg have a permanent and reproducing occurrence of at least one species of large carnivore (Fig. 1). The total area with a permanent presence of at least one large carnivore species in Europe covers 1,529,800 km<sup>2</sup> (roughly one-third of mainland Europe), and the area of occasional presence is expanding, as the presence of solitary dispersing wolves has been confirmed in both Denmark and Belgium in recent times.

Brown bears presently occur permanently in 22 countries (485,400 km<sup>2</sup>) and can be clustered into 10 populations, most of which are native populations (tables S1 to S3). Eurasian lynx presently occur permanently in 23 countries (813,400 km<sup>2</sup>) and can be clustered into 11 populations, five of them being native populations (tables S5 to S7). Wolves currently occur permanently in 28 countries (798,300 km<sup>2</sup>) and can be clustered into 10 populations, which are all native (tables S9 to S11). Wolverines, however, are only found in the three Fennoscandic countries, and they permanently occur over a total of 247,900 km<sup>2</sup> in two populations (tables S13 to S15). Because of the limited biogeographic distribution of wolverines, Fennoscandia is the only region containing all four large carnivore species in Europe (171,500 km<sup>2</sup>), and could be considered as a large-carnivore hot spot together with southeastern Europe (Dinaric, Carpathian, and Balkan regions) and the Baltics (fig. S2). Three large carnivore species overlap over 593,800 km<sup>2</sup> in Europe (fig. S2).

Overall, Europe hosts several large and stable populations on the order of thousands of individuals, many medium-sized and increasing populations that number in the hundreds of individuals, and a few small and declining populations with a few tens of individuals. Interestingly, none of the medium or large populations are declining. Brown bears are the most abundant large carnivore in Europe, with an estimated total number around 17,000 individuals, and all population ranges have

been relatively stable or slightly expanding (table S2). Wolves are the second most abundant species, with an estimated total number larger than 12,000 individuals (table S10). Most populations have been increasing or stable during recent years, although the Sierra Morena population (Spain) is on the brink of extinction, with only one pack detected in 2010 (9). In recent years, the larger Iberian population has an uncertain trend, although it seems stable, and the Karelian population has declined (9). The estimated total number of Eurasian lynx is around 9000 individuals (table S6), and most populations have generally been stable in the past decade, although most of the reintroduced populations appear to have stagnated at relatively small sizes, and the Vosges-Palatinian and Balkan lynx populations have declined (9). Finally, the estimated total number of wolverines is 1250 individuals, and both populations are increasing (table S14). Details on large carnivore monitoring methods are given in tables S4, S8, S12, and S16 and (9).

All four large carnivore species are persisting in human-dominated landscapes (fig. S3) and largely outside protected areas. The mean  $\pm$  SD human density in areas of permanent large carnivore presence is  $19.0 \pm 69.9$  inhabitants/km<sup>2</sup> (range: 0 to 1651) for brown bears;  $21.8 \pm 73.8$  inhabitants/km<sup>2</sup> (range: 0 to 2603) for lynx;  $36.7 \pm 95.5$  inhabitants/km<sup>2</sup> (range: 0 to 3050) for wolves; and  $1.4 \pm 5.7$  inhabitants/km<sup>2</sup> (range: 0 to 115) for wolverines (fig. S3). These figures suggest species-specific sensitivities of large carnivores to humans, with wolves being most successful in adapting to human-dominated landscapes (fig. S3). Wolverines are somewhat special, because their distribution is constrained by climatic conditions, which restricts them to northern and high-altitude areas, which have low human population densities (10).

These figures permit cautious optimism for the occurrence, abundance, and trends for large carni-

vores in Europe. The general picture emerging from the current status of large carnivores in Europe is that these species have shown the capacity to survive in human-dominated landscapes, representing an often underappreciated conservation success story. Having high numbers of large carnivores in such landscapes is not exclusive to Europe [the United States has abundant populations of black bears (*Ursus americanus*) and mountain lions (*Puma concolor*)]; however, the largest species, brown bears and wolves, occur in Europe with much higher human densities. For example, Europe hosts twice as many wolves (>11,000) as the contiguous United States [ $\sim$ 5500 wolves (11)], despite being half the size (4.3 million km<sup>2</sup> versus 8 million km<sup>2</sup>) and more than twice as densely populated (97 inhabitants/km<sup>2</sup> versus 40 inhabitants/km<sup>2</sup>).

We believe that the alternative view to the coexistence model (i.e., the separation model), which argues that the largest predators can only survive in protected areas or wilderness, is a consequence of former policy goals to exterminate these species (12). However, our results underline that if the separation model had been applied in Europe, there would hardly be any large carnivore populations at all, because most European protected areas are too small to host even a few large carnivore reproductive units (13).

Whereas large carnivores do not permanently occur in the areas of highest human density in Europe, they have shown an ability to recolonize areas with moderate human densities if they are allowed, and to persist in highly human-dominated landscapes and in the proximity of urban areas (14, 15) in highly fragmented landscapes consisting of forest-farmland mosaics or even agroecosystems. Our results are not the first to reveal that large carnivores can coexist with people (16–18), but they show that the land-sharing model for large carnivores (coexistence model) can be successful on a continental scale.

The reasons for the success of large carnivores in Europe range from coordinated legislation shared by many European countries (19, 20) to context-specific management practices and institutional arrangements. Since the end of World War II, Europe has benefited from stable political institutions ensuring proper law enforcement. The post-communist transition in Eastern European countries was not generally associated with institutional collapse, with the exception of some Balkan countries. This stability created the conditions for securing land tenure and associated rights for activities such as forestry and hunting, which are preconditions for the development of sustainable practices. The rise of environmental movements in the 1970s provided the motivation for various pan-European legislative agreements to emerge that served to promote biodiversity conservation. For example, the Bern Convention, administered by the Council of Europe, covers all countries included in this report, and the Habitats Directive covers all 20 European Union member states with a permanent occurrence of large carnivores. Consequently, the four large carnivore species examined here enjoy some degree of legal protection in all European countries. Large carnivores have also benefited from the socioeconomic changes over the past four decades that led to an improvement in habitat quality. For example, Europe again hosts large populations of wild ungulates (21), which can sustain large carnivore populations. The impact of human land-use activities has also been declining in many areas because of a widespread exodus from rural areas and the associated abandonment of agricultural land (22). These broad patterns are further accompanied by a variety of local, cultural, or regulatory practices making coexistence between large carnivores and people possible (15, 23). One important prerequisite has been to maintain and revive traditional livestock protection measures

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(livestock-guarding dogs, night corrals, and shepherd herds), as well as to invest in new techniques (electric fences) as an important nonlethal tool to minimize large carnivore depredation on livestock (24).

The most severe challenges for large carnivore conservation are in countries where large carnivores have previously been extirpated, where the adaptations for coexistence have been lost, or where husbandry practices have evolved toward new production schemes. In such contexts, the return of large carnivores can trigger social conflicts. For example, poaching enjoys social acceptance in rural areas of Norway (25), limits the recovery of wolves in Scandinavia (26), and eradicated a reintroduced bear population in Austria (27). In these areas, the practical challenges and economic impacts of carnivore conservation have escalated into social conflicts, where the carnivores have become symbols of wider political divisions between rural and urban populations and between individuals and groups with fundamentally different value orientations and interests.

At present, there is a conjuncture between many policy areas combined with a generally supportive public opinion, so that the positive forces have been prevailing. However, the underlying negative forces are still present and could reemerge as a result of ecological, social, political, or economic changes. There is a need to monitor both the ecological situation and sociopolitical climate to ensure that the current trends are maintained.

The European experience offers hope for wildlife conservation in human-dominated landscapes and is relevant to other areas of the world. Although developing countries may lack many of the institutions and capacities that have enabled large carnivore recovery in Europe, there are other examples of large carnivores persisting and recovering in human-dominated landscapes and even in cities (17, 28, 29). Clearly, the presence of large carnivores in human-dominated ecosystems is associated with modified ecological conditions that deviate from conditions in areas with little human activity. However, the fact that such species

can persist in these novel ecosystems encourages optimism for the conservation of larger and more connected large carnivore populations.

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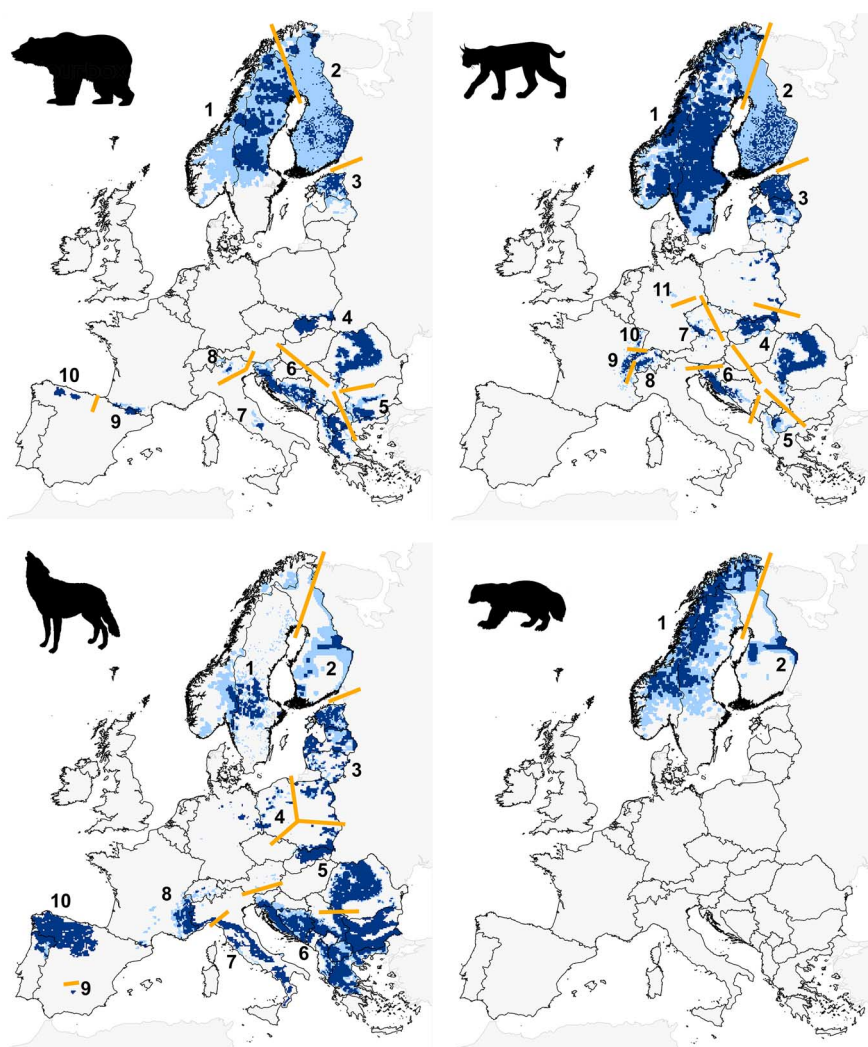
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**Fig. 1. Distribution of large carnivores in Europe in 2011.** Brown bears (top left), Eurasian lynx (top right), gray wolves (bottom left), and wolverines (bottom right). Dark blue cells indicate areas of permanent occurrence, and light blue cells indicate areas of sporadic occurrence. Numbers refers to population identifications in tables S1 to S16. Orange lines indicate boundaries between populations.



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